The anuran tarsus

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The structure of the tarsus in adult specimens and larval sequences in different families of anurans are analyzed, in order to establish an overall concept of the diversity of this character in the group. Ontogenetic analysis has made it possible to confirm the hypothesis of the origination of distal tarsals and metatarsals along the fibular axis, whereas the element Y and the prehallux originate along the tibial axis, with no differentiation into intermedium nor centralia. On the basis of ontogenetic information, it can be established that the plesiomorphic condition of the tarsus in anurans is that in which the ends of the tibiale and fibulare are fused, and there are three free distal tarsals, the element Y and the prehallux. Apomorphic states can be recognized by different types of fusion between proximal and distal elements, or by a reduction of distal elements.

INTRODUCTION

The anuran tarsus is one of the most characteristic structures of the group, due to its degree of specialization. Although both anatomical and functional studies have been carried out for many years, there is still debate over tarsus homologies, the embryonic elements making up the structure, and the evolution of the latter in anurans

HOWES & RIDEWOOD (1888) described four different tarsal morphologies in various species of extant anurans from a strictly anatomical point of view. LAURENT (1940, 1941a-b, 1942), LIEM (1970) and DREWES (1984) described two of these in the Arthroleptidae, Ranidae and Rhacophoridae. All these authors recognized differences in the distal portions of the tarsus. ANDERSEN (1978) presented an hypothesis of tarsal evolution in anurans based on five patterns that include variations in both proximal and distal areas of the tarsus. The above-mentioned studies rest on observations carried out on postmetamorphic specimens, and all concur in pointing out a tendency toward reduction of the number of individual elements.

HOLMGREN (1933), TRUEB (1973) and JAROSOVA (1974) refer to fusion of the intermedium with the proximal end of the tibiale, whereas up to four embryonic centralia fuse with the distal tarsals during development These hypotheses are very different from those put forward by other authors (HOWES & RIDEWOOD, 1888; SHUBIN & ALBERCH, 1986), who claim that there is no trace of the intermedium during anuran limb ontogeny.

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According to HOWES & RIDEWOOD (1888), the only central element recognized in the tarsus corresponds to the proximal element of the prehallux, whereas SHUBIN & ALBERCH (1986) denied the existence of centralia in the anuran autopodium. With regard to the distal tarsals, there is coincidence in the descriptions which indicate the presence of the distal tarsals 3, 2 and 1, and there is evidence of appearance of discrete cartilaginous foci of the distal tarsals 5 and 4 during development in some species.

All this somewhat controversial information leads to the conclusion that it is necessary to investigate the tarsus in this group in greater depth.

The present work analyzes the tarsus in specimens from different families, in order to obtain an overall view of the structure and distribution of adult morphology. Furthermore, some sequences of tarsal development are analyzed, in the hope of dispelling some doubts raised by the information currently available.

MATERIAL AND METHOD

The adult specimens and larvae listed in Appendix were analyzed. Ontogenetic series were staged according to GOSNER (1960). All the sample specimens were prepared according to the technique proposed by WASSERSUG (1976) for whole preparations. The tadpole hindlimbs were dissected and placed on slides.

Observations, drawings and photomicrographs of whole mounts were made using stereo-microscope with camera lucida and darkfield microscope.

Tarsus descriptions were made using the terminology in SHUBIN & ALBERCH (1986).

The following abbreviations were used in figures. d1, distal tarsal 1; d2, distal tarsal 2; d3, distal tarsal 3, Fe, femur, F, fibula; F1, fibulare; LO, plate osseous; Ph, prehallux; s?, sesamoid; T, tibia; Ti, tibiale; Y, element Y; I, metatarsal I; II, metatarsal II; III, metatarsal III; IV, metatarsal IV; V, metatarsal V.

RESULTS

ARTHROLEPTIDAE (ASTYLOSTERNINAE, ARTHROLEPTINAE AND HYPEROLIINAE, SENSU LAURENT, 1986)

Adult specimens of the genera *Afrixalus, Arthroleptis, Astylosternus, Cardioglossa, Hyperolus, Kassina, Leptopelis, Phlyctimantis, Opisthothylax* and *Schoutedenella* were analyzed.

Cardioglossa cyaneospila and *C leucomystax* were observed to have the tibiale and fibulare fused at the ends, the distal tarsals 3, 2 and 1 articulating with the metatarsals III, II and I, and the element Y and the prehallux both present. The prehallux is formed of one element in *C. cyaneospila* and three elements in *C. leucomystax* (fig. 1 A).
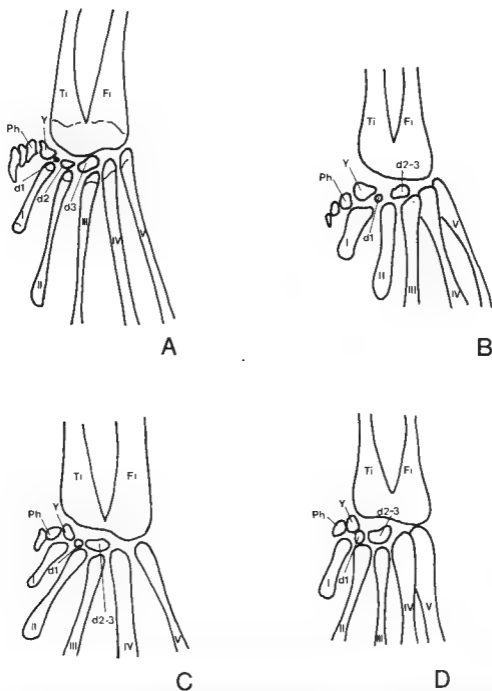
Fig. 1. (A) Dorsal view of right foot of *Cardioglossa leucomystax*. (B) Dorsal view of right foot of *Bufo granulosus*. (C) Dorsal view of right foot of *Dendrobates pictus*. (D) Dorsal view of right foot of *Pleurodema cinerea*.

In the remaining members of this family, the structure of the tarsus was characterized by the fusion of the ends of the tibiale and fibulare, the distal tarsal 3-2 articulating with the metatarsals III and II, the distal tarsal 1 articulating with the metatarsals II and I, and the presence of the element Y and the prehallux In *Afrixalus quadrivittatus*, *Arthroleptis poecilonotus*, *A. stenodactylus*, *A. variabilis*, *Leptopelis christyi* and *Opisthothylax* sp., the prehallux consists of a single element; in the remaining species it consists of two elements.

BUFONIDAE

Adult specimens of the genera *Atelopus*, *Bufo* and *Melanophryniscus* were analyzed The tarsus is formed of the tibiale and fibulare fused at the ends, the distal tarsal 3-2 articulating with the metatarsals III and II, the distal tarsal 1 articulating with the metatarsals II and I, the element Y and the prehallux. The prehallux consists of one element in *Melanophryniscus r. rubriventris*, two elements in *Atelopus pachyrhinus* and three elements in *Bufo granulosus* (fig. 1 B).

DENDROBATIDAE

The tarsus of an adult specimen of *Dendrobates pictus* (fig. 1 C) was analyzed, and found to present fusion of the ends of the tibiale and fibulare, the distal tarsal 3-2 articulating with the metatarsals III and II, the distal tarsal 1 articulating with the metatarsal II and I, the element Y, and the prehallux formed of two elements.

HEMISOTIDAE

The tarsus of an adult specimen of *Hemisus g guineensis* was analyzed. It presented the tibiale and fibulare fused at the ends, the distal 3-2 articulating with the metatarsals III and II, the distal tarsal 1 articulating with the metatarsals II and I, the element Y, and the prehallux formed of one element.

HYLIDAE

Adult specimens of the genera *Argenteohyla*, *Gastrotheca*, *Hyla*, *Phyllomedusa*, and *Scinax* (DUELLMAN & WIENS, 1992) were analyzed, together with larval preparations of *Hyla pulchella andina* and *Phyllomedusa sauvagii* (fig. 2 A).

The tarsus of all the adult hylids analyzed was formed of the tibiale and fibulare fused at the ends, the distal tarsal 3-2 articulating with the metatarsals III and II, the distal tarsal 1 articulating with the metatarsals II and I, the element Y and the prehallux The number of pieces in the prehallux varied according to the species: two in *Argenteohyla siemersii*, *Scinax nasica* and *Phyllomedusa hypochondrialis*, and three in the remaining species

In the preparations of the larval limbs from *Hyla pulchella andina* and *Phyllomedusa sauvagii*, it was observed that the fibulare differentiates earlier than the tibiale. Together
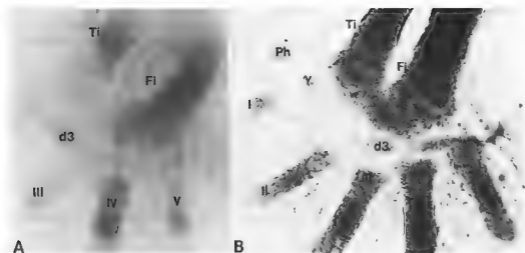
Fig. 2. – (A) Early stage of the tarsus development in *Phyllomedusa sauvagii*, in which rudiments of tibiale, fibulare, metatarsals IV, III and V and the distal tarsal 3 condensation are present. (B) Advanced stage of the tarsus development in *Leptodactylus* cf *gracilis*, in which distal tarsal 3, element Y, prehallux, five metatarsals and fused tibiale and fibulare are present.

with the two proximal tarsal rudiments (tibiale and fibulare), the metatarsal IV rudiment is also present. In the next stage, the metatarsals V and III appear, and a proliferation at the end of the fibulare becomes apparent, from which the cartilage condensation corresponding to the distal tarsal 3 arises. Later, when the metatarsal II and I rudiments are formed, the element Y condensation and the beginning of fusion between the tibiale and fibulare can be seen. Finally, the distal tarsal 2 differentiates as a continuation of the distal tarsal 3, while the distal tarsal 1 and the prehallux elements differentiate in a distal direction.

LEIOPELMATIDAE

Only two larval specimens of *Ascaphus truei* with ages corresponding to stages 39 and 42 of GOSNER (1960) were analyzed. As these stages are advanced in regard to limb development, no embryonic connections between the elements, such as those described by SHUBIN & ALBERCH (1986), were observed.

The stage 39 tadpole showed a cartilaginous tibiale and fibulare, fused at their ends; five distal tarsals (1, 2, 3, 4 and 5) diminishing in size in an anterior direction; the element Y located between the distal end of the tibiale; and a small condensation corresponding to the proximal segment of the prehallux. Each of the distal tarsals is related to the corresponding metatarsal.

The stage 42 tadpole showed the fusion of distal tarsals 5 and 4 with the distal end of fibulare (this can be deduced from the elongation of the distal end of the fibulare which

exceeds the tibiale in length). The metatarsals V and IV articulated directly with the end of the fibulare, while the metatarsals III, II and I maintained their relationship with the corresponding distal tarsals. The element Y was larger in size than the distal tarsals and supported the proximal element of the prehallux, made up of the two elements.

The morphology described for the stage 42 tadpole is the same as that described by ANDERSEN (1978) for an adult of *Ascaphus truei*.

LEPTODACTYLIDAE

Adult specimens of the genera *Eleutherodactylus, Hylodes, Leptodactylus, Odontophrynus, Pleurodema* and *Syrrhopus* were analyzed, as were ontogenetic series of *Leptodactylus, Odontophrynus* and *Pleurodema*.

The tarsal morphology of the adults is similar in all these species, with variations observed at the level of the number of prehallux elements. The tibiale and fibulare are fused at the ends, the metatarsals V and IV articulate directly with the end of the fibulare, the distal tarsal 3-2 articulates with the metatarsals III and II, the distal tarsal 1 articulates with the metatarsals II and I, and the element Y and the prehallux are present. The prehallux in *Leptodactylus podicipinus, Pleurodema cinerea* (fig. 1 D) and *Syrrhopus nivicolimae* is formed of a single element. In *Eleutherodactylus discoidalis, Hylodes nasus, Leptodactylus chaquensis, L. fuscus, L. gracilis* and *Odontophrynus occidentalis*, the prehallux is formed of two elements. In the rest of the species three elements were observed.

The sequences of tarsal development analyzed in the species of Leptodactylidae studied (fig. 2 B) is similar to that described for the Hylidae.

MICROHYLIDAE

Adult specimens of the genera *Breviceps, Dermatonotus* (fig. 3 A), *Elachistocleis, Gastrophryne,* and *Phrynomantis* (DUBOIS, 1988) were analyzed, as were ontogenetic series of the limb in *Dermatonotus muelleri*.

Observation of the tarsus in these species showed the tibiale and fibulare fused at the ends, the distal tarsal 3-2 articulating with the metatarsals III and II, the distal tarsal 1 articulating with the metatarsals II and I, the element Y and the prehallux. In all of them the prehallux consisted of two pieces.

The only difference in limb development observed in *Dermatonotus muelleri* was that the fusion of the ends of the tibiale and fibulare takes place prior to differentiation of the distal tarsals and of the element Y.

MYOBATRACHIDAE

Adult specimens of the genera *Crinia* (fig. 3 B), *Limnodynastes* and *Neobatrachus* were analyzed. The tarsal morphology observed is characterized by the presence of: tibiale and fibulare fused at the ends; metatarsal V and IV articulating directly with the end of the

fibulare; distal tarsal 3-2 articulating with metatarsal III and II; distal tarsal 1 articulating with metatarsals II and I; element Y and prehallux, this last formed of two elements. The distal segment of the prehallux in *Neobatrachus pictus* is greatly developed.

PELODYTIDAE

An adult specimen of *Pelodytes punctatus* (fig. 3 C) was analyzed. It has the tibiale and fibulare fused along their entire length, although a groove remains between the two elements, revealing their dual nature. Present are the distal tarsals 3, 2 and 1, which articulate with the corresponding metatarsals, whereas the metatarsals V and IV articulate with the distal end of the fibulare. The distal tarsal 3 is the largest of the set. The element Y supports the prehallux, formed of three pieces. HOWES & RIDEWOOD (1888) describe the same tarsal morphology for this species, and TALAVERA (1985) analyzed its development. This last author observed that the specialization in *Pelodytes punctatus* includes not only the complete fusion of tibiale and fibulare, but also an early beginning of the ossification and fusion of these elements, a characteristic notably different from any observed in other species.

PIPIDAE

Adult specimens of the genera *Xenopus*, *Hymenochirus* and *Pipa* were analyzed.

In *Xenopus*, the tibiale and fibulare are fused at the ends and they are of equal length. The metatarsals V and IV articulate directly with the distal end of the fibulare. There are two distal tarsals: the distal tarsal 3-2 which articulates with the metatarsals III and II; and the distal tarsal 1 — somewhat smaller in size — which articulates with the metatarsals II and I. There is the element Y related to the tibiale, the distal tarsal 1 and the metatarsal I, and supporting the prehallux formed of two elements. HOWES & RIDEWOOD (1888) describe this same morphology in *Xenopus laevis*, the only difference being their observation of the prehallux with three elements.

In *Hymenochirus boettgeri camerunensis* (fig. 3 D), the tibiale and fibulare are completely fused, with the small fissure between them. The metatarsals V and IV articulate directly with this osseous complex. The distal tarsals 3-2 and 1, and the element Y, are observed to be the same as in *Xenopus*, but no elements which can be assigned to the prehallux are evident. Five or six sesamoids are present in plantar position between tibiale-fibulare and metatarsals.

In *Pipa*, the ends of the tibiale and fibulare are joined by a thin ossification. In dorsal view, the five metatarsals are articulated to a broadened osseous plate. In the ventral view, there are osseous condensations between the tibiale-fibulare and the metatarsals. four in *Pipa parva* (fig. 4 A) and six in *P. carvalhoi*, with no prehallux present. HOWES & RIDEWOOD (1888) observed a similar tarsal structure in *P. pipa*, where the metatarsals V and IV articulated directly with the end of the fibulare, while the remaining metatarsals articulated with the osseous plate (which is preaxial in this species). Three osseous condensations were observed in ventral view. The above-mentioned authors considered
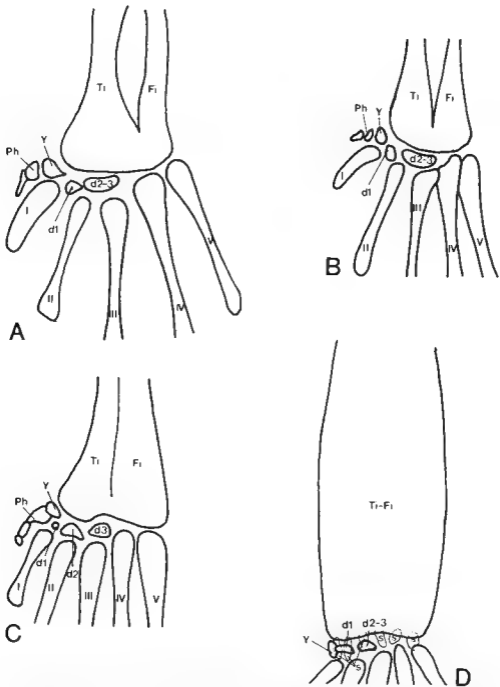
Fig. 3. — (A) Dorsal view of right foot of *Dermatonotus muelleri*. (B) Dorsal view of right foot of *Crinia signifera*. (C) Dorsal view of right foot of *Pelodytes punctatus*. (D) Dorsal view of right foot of *Hymenochirus boettgeri camerunensis*.
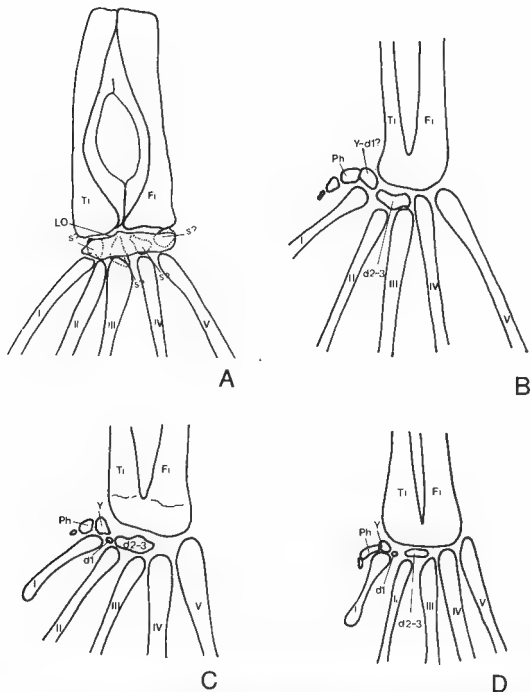
Fig. 4. - (A) Dorsal view of right foot of *Pipa parva*. (B) Dorsal view of right foot of *Chiromantis rufescens*. (C) Dorsal view of right foot of *Phrynobatrachus petropedetoides*. (D) Dorsal view of right foot of *Rhinoderma darwinii*.

these condensations to correspond to the distal tarsal 3-2, the element Y and a sesamoid. It is difficult to interpret the homologies of these structures in *Pipa*, because their tarsal-metatarsal union is highly altered. The size of the bony dorsal plate varies, as do the number of osseous condensations, but it may be that both the plate and these condensations have no relation to the original tarsal elements, and are really sesamoids, similar to those observed in *Hymenochirus boettgeri camerunensis*. However, it will require a closer study of all aspects of the development and variation of the tarsal structure in these species to be carried out before any feasible interpretation can be made.

PSEUDIDAE

Adult specimens of the genera *Lysapsus* and *Pseudis* were analyzed. They were observed to have a tarsus made up of tibiale and fibulare fused at the ends, the distal tarsal 3-2 articulating with the metatarsal III and II, the distal tarsal 1 articulating with the metatarsals II and I, the element Y and the prehallux. The prehallux in both genera was composed of two elements, the distal one being very developed.

RANOIDAE (MANTELLIDAE, PHRYNOBATRACHIDAE AND RANIDAE, SENSU DUBOIS, 1992)

Adults specimens of the genera *Aubria*, *Chiromantis*, *Hoplobatrachus*, *Phrynobatrachus* and *Ptychadena* were analyzed.

Most of the Ranoidae examined present a similar tarsal morphology, consisting of the tibiale and fibulare fused at the ends, the distal tarsal 3-2 articulating with the metatarsals III and II, a very small distal tarsal 1 articulating with the metatarsals II and I, the element Y and the prehallux.

The presence of a free distal tarsal 1 is not observed in *Chiromantis rufescens* (fig 4 B), *Phrynobatrachus natalensis* and *P asper*. Its absence can be interpreted as a loss, or as a fusion with some other element, probably the element Y.

There are variations in the number of pieces in the prehallux. This is formed of one element in *Phrynobatrachus acutirostris* and *P. petropedetoides* (fig. 4 C), and in the remaining species of two elements — with the exception of *Aubria subsigillata*, in which it is formed of three.

RHINODERMATIDAE

One adult specimen of *Rhinoderma darwinii* (fig. 4 D) was analyzed. It presented a tarsus consisting of the tibiale and fibulare fused at the ends, the distal tarsal 3-2 articulating with the metatarsals III and II, the distal tarsal 1 articulating with the metatarsals II and I, the element Y, and the prehallux formed of two pieces.

DISCUSSION

As pointed out in the introduction, the existing information on tarsal development in the anurans is contradictory.

SHUBIN & ALBERCH (1986) have proposed a tentative development model for the anuran limb. This model explains the differentiation of autopodium elements in a proximal-distal and posterior-anterior direction on the basis of two cartilaginous series (postaxial and preaxial), in which processes such as branching, segmentation and de novo condensation are seen (fig. 5). The postaxial series (corresponding to fibula) segments to the fibulare; at the distal end of the fibulare there is an area of differentiation of distal tarsal 4 and metatarsal IV (distal tarsal 5 being formed by de novo condensation) Distal tarsal 4 does not segment from the end of fibulare, but branches to form distal tarsal 3. Distal tarsal 3 branches and segments to form metatarsal III and distal tarsal 2, metatarsal II arising from the last. Distal tarsal 1 could be formed by de novo condensation   as could metatarsal I — or could be cleaved from distal tarsal 2. On the other hand, the preaxial series (corresponding to the tibia) segments form the tibiale, the element Y and the prehallux. According to the above-mentioned authors, in the tetrapods, the intermedium differentiates from the branching end of the fibula together with the fibulare, while the centralia segments from branches of the intermedium. This does not occur in the anurans.

The results of the present work on tarsal development in various species of anurans confirm the model proposed by SHUBIN & ALBERCH (1986), as no trace of cartilage condensation which could be attributed to the intermedium and/or centralia were observed. The differentiation of the preaxial elements — tibiale, element Y and prehallux — in a proximal-distal sequence has been confirmed. A description has also been given, in a proximal-distal and posterior-anterior sequence, of the differentiation of the postaxial elements: namely, fibulare, distal tarsals and metatarsal V to I.

Although the results obtained herein support the hypothesis of the non-existence of intermedium and centralia during tarsal development in the anurans, they are not exhaustive enough to entirely negate the results obtained by other authors (especially JAROSOVA, 1974). This last author made a careful analysis of the hindlimb development of *Xenopus laevis* and *Discoglossus pictus* by studying histological preparations of larval limbs, in which she observed the presence of these condensations.

An analysis of the development patterns shows that the individual tarsals which can be recognized in the early stages of hindlimb differentiation are the tibiale, the fibulare, the distal tarsals 3, 2 and 1, the element Y and the prehallux The progressive fusion of some of these can be verified in the later ontogenetic stages of some species. This leads to the supposition that the plesiomorphic condition of the tarsal structure is that of the initial stages of limb differentiation, and is that presented by the adult forms of the Leiopelmatidae, Discoglossidae (HOWES & RIDEWOOD, 1888, ANDERSEN, 1978), Pelobatidae (HOWES & RIDEWOOD, 1888; ANDERSEN, 1978) and two species of *Cardioglossa*.

Subsequent to this plesiomorphic condition of the tarsus, in which all the elements can be individually recognized, progressive fusions between them take place during the
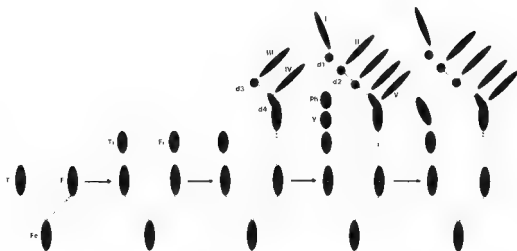
Fig. 5. – Schematic sequence of the tarsus development in *Xenopus laevis* (from SHUBIN & ALBERCH, 1986), reduced to patterns of branching, segmentation and de novo condensation.

development, leading to the appearance of apomorphic states in different directions that are characteristic of the adults. In one direction, as observed in the Pelodytidae, there is complete fusion of the tibiale and of the fibulare, which is further associated with other specializations (TALAVERA, 1985). Alternatively, in another direction arises the apomorphic state represented by fusion of the distal tarsals 3 and 2.

This last condition is amply distributed throughout the remaining families, including Pelobatidae (HOWES & RIDEWOOD, 1888; LYNCH, 1973; ANDERSEN, 1978; DUELLMAN & TRUEB, 1985).

In the Pipoidea, the *Xenopus* tarsus represents the generalized condition from which at least two apomorphic, apparently independent, states will emerge. (1) In the *Pipa* species analyzed in this work, and in that of HOWES & RIDEWOOD (1888), the replacement of the distal tarsals, of the element Y and of the prehallux by a complex formed of an osseous plate and a set of sesamoids has been observed. (2) In *Hymenochirus boettgeri camerunensis*, the condition of the fused tibiale and fibulare and reductions of the prehallux elements (with the distal tarsals 3-2 and 1 and the element Y preserved, as in *Xenopus*), with sesamoids associated, is present. Another state observed in the tarsal structure of Pipoidea is that described by ANDERSEN (1978) as found in *Rhinophrynus dorsalis*, in which only the tibiale and fibulare are preserved as tarsal elements.

The morphology described for the majority of the Myobatrachidae species (LYNCH, 1973; ANDERSEN, 1978; GOLLMANN, 1991) is similar. However, in hybrid populations of *Geocrinia laevis* and *Geocrinia victoriana* (GOLLMANN, 1991), there are numerous variations in the shape and number of tarsal elements. These include complete fusions (with or without signs of suturing) between distal tarsals, hypertrophy of the element Y, the appearance of accessory elements, and so on. In some cases these variations are symmetric.

In the Brachycephalidae, Bufonidae, Centrolenidae, Hylidae, Leptodactylidae, Microhylidae, Pseudidae and Rhinodermatidae, the presence of three free distal tarsals has been mentioned only for the Rhinodermatidae by LYNCH (1971) and DUELLMAN & TRUEB (1985). This information is different from that obtained from analysis of the *Rhinoderma darwinii* tarsus in the present work and in that of ANDERSEN (1978). According to the results here given, the condition of the tarsus in these families includes the presence of the tibiale and fibulare fused at the ends, the distal tarsals 3-2 and 1, the element Y and the prehallux (with a variable number of elements). According to reference data, two independent apomorphic states can emerge from this condition, as shown by complete fusion of tibiale and fibulare occurring in Centrolenidae (LYNCH, 1973; ANDERSEN, 1978; DUELLMAN & TRUEB, 1985) and *Geobatrachus* (DUELLMAN & TRUEB, 1985).

DREWES (1984) analyzed the tarsus in Ranoidea and recognized the following character states: (0) distal tarsals not fused; Leiopelmatidae, Discoglossidae and *Pelodytes*; (1) distal tarsals 3 and 2 fused; all Ranoidea except Hyperoliinae; (2) distal tarsals not fused (paedomorphic); Hyperoliinae.

This author established the polarity in the $0 \to 1 \to 2$ direction. Furthermore, he recognized other states in regard to the distal tarsal 1, namely: (0) presence of the distal tarsal 1, plesiomorphic; Astylosterninae, Arthroleptinae, *Arthroleptella, Cacosternum, Strongylopus, Ptychadena, Rana* (African species), and *Hemisus*; (1) absence of the distal tarsal 1 in free form (it can be absent or fused to the element Y), apomorphic; Phrynobatrachidae, *Abrana, Aubria, Hylarana, Tomopterna, Pyxicephalus,* and Hyperoliinae.

Owing to the fact that DREWES (1984) did not illustrate his observations, it is difficult to interpret his results, as even analyses carried out on the same species give different results. The present writer considers that the unfused condition of distal tarsals 3 and 2 which DREWES (1984) attributes to the Hyperoliinae is not exact, and that what the latter interprets as the distal tarsal 2 (as opposed to the interpretation he gives for Ranoidae) is the distal tarsal 1 of the present work. With regard to the absence of the distal tarsal 1 in *Aubria* and the Phrynobatrachidae, this would also seem to be an error; according to observations made in the present work, only two species of *Phrynobatrachus* lack a free distal tarsal 1. In the Hyperoliinae, as well as in the Astylosterninae, Arthroleptinae, Ranidae, Phrynobatrachidae and Hemisotidae, the distal tarsal 1 is present. The only notable difference with regard to this element is that in *Aubria* and the Phrynobatrachidae it is proportionally much smaller than the distal tarsal 3-2 and the element Y. These results lead to the interpretation — identical to that of LAURENT (1940, 1941a-b, 1942) — that the fusion of the distal tarsals 3 and 2 is a widely distributed condition, as is the presence of the distal tarsal 1. Only *Cardioglossa* among the ranoids exhibits a clearly plesiomorphic condition with respect to the tarsus. In the remainder of the Arthroleptinae, as well as in the Astylosterninae, Hyperoliinae, Ranidae, Phrynobatrachidae and Hemisotidae analyzed, the condition of the tarsus is derived from that of *Cardioglossa* by fusion of the distal tarsals 3 and 2. The state observed in *Phynobatrachus asper, P. natalensis* and *Chiromantis rufescens*, where the distal tarsal 1 is absent, probably due to fusion with the element Y as observed in the development of *Rana catesbeiana* (HOWES & RIDEWOOD, 1888), would in turn derive from the foregoing state.

With regard to the structure of the prehallux, an interspecific variation in the number of elements it contained was observed. Although only a small number of specimens were analyzed for each species, from information supplied by other authors (HOWES & RIDEWOOD, 1888; ANDERSEN, 1978) it is probable that this structure also varies intraspecifically with relation to sex and age. However, the absence of a prehallux in Pipoidea, which shows a highly specialized tarsal structure, could also be considered an apomorphy.

CONCLUSIONS

(1) On the basis of an analysis of the hind limb ontogeny, it can be suggested that the plesiomorphic condition of the anuran tarsus is shown by the presence of the tibiale and fibulare fused at the ends, three free distal tarsals (3, 2 and 1), the element Y and the prehallux.

(2) The apomorphic states result from the fusion of proximal and/or distal tarsal elements, or from reduction of distal elements.

(3) The Pipoidea show the greatest complexity and specialization in their tarsal structure. In these forms the typical tarsal elements are replaced by others.

RESUMEN

Se analiza la estructura del tarso en especímenes adultos y secuencias larvales de diferentes familias de anuros con el propósito de establecer un panorama global de la diversidad de este carácter en el grupo. El análisis de la ontogenia permite confirmar la hipótesis del origen de los tarsales distales y metatarsales a partir del eje fibular, mientras que el elemento Y y el prehallux se originan del eje tibial, sin diferenciación de intermedio y centrales. Sobre las bases de la información ontogenética, se puede establecer que la condición plesiomórfica del tarso en los anuros es aquella en la que los extremos del tibial y fibular se encuentran fusionados, y existen tres tarsales distales libres, el elemento Y y el prehallux. Los estados apomórficos pueden ser reconocidos por diferentes tipos de fusión entre los elementos proximales y distales, o por la reducción de los elementos distales.

ACKNOWLEDGEMENTS

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APPENDIX

LIST OF SPECIMENS EXAMINED

FML: Fundación Miguel Lillo, Tucumán.
RFL: personal collection of Raymond F. LAURENT, Tucumán
MCN: Museo de Ciencias Naturales, Universidad Nacional de Salta.

Staging of larvae is according to GOSNER (1960).

Family ARTHROLEPTIDAE (= HYPEROLIIDAE sensu LAURENT, 1986).
    Subfamily ARTHROLEPTINAE. – *Arthroleptis adolfifriederici*: RFL 90c (3 specimens); *Arthroleptis poecilonotus*: RFL 232h (2 specimens); *Arthroleptis stenodactylus*: RFL 108b (1 specimen), *Arthroleptis variabilis* RFL 143 (1 specimen); *Cardioglossa cyaneospila*: RFL 66a (2 specimens), *Cardioglossa leucomystax*: RFL 170 (2 specimens), *Schoutedenella pyrrhoscelis*: RFL 121 (4 specimens); *Schoutedenella schubotzi*. RFL 175b (4 specimens); *Schoutedenella sylvatica*: RFL 169b (2 specimens), RFL 43b (2 specimens).
    Subfamily ASTYLOSTERNINAE   *Astylosternus diadematus* FML 03215 (2 specimens).
    Subfamily HYPEROLIINAE. – *Afrixalus laevis*: RFL 16g (1 specimen), RFL 92a (1 specimen); *Afrixalus osorioi*. RFL 4 (2 specimens), RFL 74 (2 specimens); *Afrixalus quadrivittatus*: RFL 44b (2 specimens); *Hyperolius castaneus*: RFL 54c (9 specimens); *Hyperolius marmoratus argentovittis*: RFL 101fg (2 specimens); *Kassina senegalensis angeli* RFL 158g (1 specimen); *Kassina senegalensis ruandae*: RFL 273 (2 specimens); *Leptopelis christyi*: RFL 135 (4 specimens), FML 3988 (1 specimen), FML 3987 (1 specimen), *Opisthothylax sp* : RFL s/n.; *Phlyctimantis verrucosus*: RFL 81b (3 specimens), RFL 87 (3 specimens)

Family BUFONIDAE. – *Atelopus pachyrhinus*: FML 3496 (1 specimen), *Bufo granulosus*: FML 4408 (1 specimen), *Melanophryniscus r. rubriventris*. FML 2502 (1 specimen), FML 1484 (1 specimen)

Family DENDROBATIDAE. – *Dendrobates pictus*: FML 3516 (1 specimen)

Family HEMISOTIDAE. – *Hemisus g. guineensis*: FML 1244 (1 specimen).

Family HYLIDAE. – *Argenteohyla siemersi*: FML 3954 (2 specimens); *Gastrotheca gracilis*. FML 2995 (1 specimen), FML 3816 (1 specimen), *Hyla minuta* FML 4282 (1 specimen), *Hyla nana*: FML 4352 (1 specimen), *Hyla pulchella andina*. FML 3812 (1 specimen), FML 4585 (16 tadpoles, stages 33-42), *Phyllomedusa hypochondrialis*: FML 0452 (2 specimens), *Phyllomedusa sauvagii*: FML 3822 (1 specimen), FML 3823 (1 specimen), FML 4090-4091 (30 tadpoles, stages 32-42); *Scinax nasica*: FML 3810 (2 specimens); FML 4407 (1 specimen).

Family LEIOPELMATIDAE.   *Ascaphus truei*: FML s/n (2 tadpoles, stages 39 and 42).

Family LEPTODACTYLIDAE. – *Eleutherodactylus discoidalis*: FML 0462 (2 specimens), FML 4405 (2 specimens); *Hylodes nasus* FML 3498 (1 specimen); *Leptodactylus chaquensis*: FML 4406 (1 specimen), FML 4537 (6 tadpoles, stages 37-42); *Leptodactylus elenae*: FML 1274 (1 specimen), *Leptodactylus fuscus* FML 1470 (1 specimen), FML 3887 (1 specimen), *Leptodactylus gracilis*: FML 2984 (1 specimen); *Leptodactylus cf. gracilis* MCN 21 (25 tadpoles, stages 32-40); *Leptodactylus podicipinus* FML 4411 (1 specimen), FML 4412 (1 specimen); *Odontophrynus americanus*: FML 1376 (1 specimen), FML 4525 (12 tadpoles, stages 35-42); *Odontophrynus lavillai*: FML 3580 (2 specimens), FML 4499 (12 tadpoles, stages 33-39), *Odontophrynus occidentalis* FML 1336 (2 specimens); *Physalaemus biligonigerus*: FML 1887 (1 specimen), FML 3930 (2 specimens), FML 1893 (2 specimens), FML 3824 (1 specimen), FML 4409 (1 specimen); *Physalaemus santafecinus*. FML 0937 (2 specimens); *Pleurodema cinerea*: FML 3785 (3 specimens); *Syrrhopus nivicolinae*: FML 1274 (1 specimen).

Family MICROHYLIDAE. – *Breviceps mossambicus*: FML 3166 (1 specimen); *Breviceps poweri* FML 3165 (1 specimen), *Dermatonotus muelleri* FML 1074 (1 specimen), FML 4571 (15 tadpoles, stages

32-42), *Elachistocleis bicolor*: FML 0251 (1 specimen), FML 4031 (1 specimen), *Gastrophryne carolinensis*: FML 3365 (1 specimen); *Gastrophryne olivacea*: FML 2384 (1 specimen); *Phrynomantis bifasciatus*: RFL 368 (3 specimens)

Family MYOBATRACHIDAE. – *Crinia signifera*: FML 3778 (1 specimen); *Limnodynastes tasmaniensis*: FML 3773 (2 specimens); *Neobatrachus pictus*: FML 3777 (1 specimen).

Family PELODYTIDAE. – *Pelodytes punctatus*: FML 3940 (1 specimen).

Family PIPIDAE. – *Hymenochirus boettgeri camerunensis*: RFL 205b (4 specimens); *Pipa carvalhoi* FML 2307 (1 specimen); *Pipa parva* FML 2856 (1 specimen), *Xenopus fraseri* RFL 186 (3 specimens); *Xenopus laevis victorianus* RFL 343 (3 specimens); *Xenopus* sp. FML 3984 (1 specimen), FML 3985 (3 specimens), FML 3986 (3 specimens).

Family PSEUDIDAE. – *Lysapsus l. limellus*. FML 0716 (1 specimen), *Pseudis paradoxa* FML 1055 (1 specimen), FML 3825 (1 specimen).

Epifamily RANOIDEA (sensu DUBOIS, 1992).
   Family PHRYNOBATRACHIDAE. – *Phrynobatrachus acutirostris*: RFL C1 (2 specimens), *Phrynobatrachus asper* RFL C18 (1 specimen), RFL C5 (2 specimens), *Phrynobatrachus dendrobates* RFL C10 (2 specimens), *Phrynobatrachus natalensis*: RFL 438 (2 specimens); *Phrynobatrachus petropedetoides*: RFL C6 (2 specimens), *Phrynobatrachus sulfureogularis*: RFL 346 (2 specimens); *Phrynobatrachus versicolor*: RFL 430 (2 specimens).
   Family RANIDAE
      Subfamily DICROGLOSSINAE — *Conraua crassipes* RFL 246 (2 specimens); *Hoplobatrachus occipitalis*: RFL 348 (1 specimen).
      Subfamily PTYCHADENINAE. – *Ptychadena aequiplicata* RFL 59 (1 specimen); *Ptychadena christyi*. RFL 76 (1 specimen); *Ptychadena chrysogaster*. RFL 141 (1 specimen), RFL 143 (1 specimen), FML 3947 (1 specimen), FML 3949 (1 specimen); *Ptychadena guibei*. RFL 163 (1 specimen), FML 3952 (1 specimen), FML 3953 (1 specimen); *Ptychadena mascarenensis bibroni*: RFL C16 (2 specimens), *Ptychadena m. mascareniensis* RFL 120 (2 specimens), RFL 123 (1 specimen), RFL 124 (1 specimen), FML 3950 (2 specimens); *Ptychadena perreti*. RFL 72 (1 specimen), RFL 99 (1 specimen); *Ptychadena porosissima*: RFL Cr1 (2 specimens); *Ptychadena uzungwensis*: RFL 157 (1 specimen)
      Subfamily PYXICEPHALINAE. — *Aubria subsigillata* RFL 209 (2 specimens), RFL 212 (1 specimen)
      Subfamily RHACOPHORINAE. – *Chiromantis rufescens* RFL 382c (2 specimens).

Family RHINODERMATIDAE. – *Rhinoderma darwinii*: FML 3694 (1 specimen)

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